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The ecology of movement in Pierid butterflies
(Lep., Pieridae)

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Introduction

BAKER (1968, 1969) examined many Palaearctic butterflies and established that most displacement in these species was voluntary. He sought an evolutionary explanation for observed differences between species and obtained a correlation between adult mobilities and the growth form and successional status of the larval foodplants. His classifications of foodplants and adult mobility were necessarily subjective and may be challenged by intensive study of any one species, e.g. *Maniola jurtina* (BRAKEFIELD, 1982); moreover his results were obtained with both sexes, despite his predictions mainly being concerned with females searching for oviposition sites. It is my purpose to record here more detailed studies and observations on a number of Pierid butterflies in Britain (1977—80) and Morocco (1978—82) which more directly address the association between larval hostplants and movement patterns.

***Anthocharis cardamines* (LINNÉ, 1758)**

The movement patterns of *A. cardamines* were studied in northern England over the period 1977—1980, as part of a larger investigation of population biology (COURTNEY, 1981; COURTNEY & DUGGAN, 1983). *A. cardamines* in this

area of Britain is localised around riverbanks, along which dispersal appears to occur. The species has greatly expanded its numbers and range in the area from the late 1960's onwards (LONG, 1980) but now seems to have stopped expansion. Mark-recapture studies on a large number of individuals of both sexes were carried out at the Durham study site, where butterflies were usually seen in the vicinity of the River Wear. Individual marks were applied to each butterfly, and its history followed. Examples of the recorded movement of a male and female were shown in Figure 1. Application of the procedure of SCOTT (1975) for analysis of recorded data yield the results shown in Table 1, whilst the frequency of observed ranges of movement (R) of either sex appear in Figure 2. It is seen that females were recorded to have moved around the study site much more freely than did males, and were recorded over wider areas. This agreed well with observations in the field: males typically patrolled a small length of riverbank, crossing and recrossing their path, as in the example in Figure 1. It appeared that individuals had a learnt home-range, in that they might be seen to repeatedly change course and turn-about at particular obstacles, such as bridges or large trees. Within their areas, males stopped occasionally to nectar and pursued any other Pierid encountered. Females, by contrast, showed no attachment to localised areas, and were often seen to leave the riverbanks where the cruciferous hosts were located (Table 2). More females also bore pollen from flowers outside the study area, than did males (COURTNEY et al., 1981), indicative of excursions away from the riverbank.

Similar differences in motility of the sexes were observed in Sweden by WIKLUND & AHRBERG (1978). In their study areas, crucifers were more generally distributed though perhaps at lower local densities. They interpreted the differences between sexes as responses to the distribution of resources – dispersed foodplants favour high mobility by females, whilst males are localised in those areas where females are most predictable. High recapture frequencies of males, as compared to females, also obtain in southern English *A. cardamines* (SHREEVE, 1981) and in the Nearctic congener *A. reakirti* (EVANS, 1955). In all *Anthocharis* populations, differential movement by the two sexes seems to fit the evolutionary advantages postulated by WIKLUND & AHRBERG. Note however that at the Durham site, crucifers are localised in a very discrete, riverside habitat, and are rarely found in the surrounding countryside. *Alliaria petiolata* (the major host) occurs in only 4 % of Co. Durham hedgerows, as compared to 60 % of hedges in southern England (BAILEY, 1979). Thus emigration of *A. cardamines* females may be less successful in the north of Britain: the species is generally confined to riverbanks in Scotland (PALMER & YOUNG, 1977) and Co. Durham (COURTNEY & DUGGAN, 1983) and colonisation of new localities seems to have taken place by movement along river courses (LONG, 1980). A high level of female movement within preferred habitats (as in Tab. 1) (which could result in colonisation along rivers) might be favoured by a number of factors:

1. A regular distribution of foodplants, so that hostplant abundance per se is fairly predictable.
2. Occupancy of oviposition sites and larval cannibalism; females usually fly long distances immediately after ovipositing an egg (COURTNEY & COURTNEY, 1982) and often respond to the presence of conspecific eggs by refusing to oviposit and flying away (WIKLUND & AHRBERG, 1978).
3. A high level of larval mortality to predators etc., will also favour females which do not aggregate their eggs in one small area, thus providing a cluster of food items for the predator. The Tachinid *Phryxe vulgaris* is a major parasitoid of Co. Durham *A. cardamines*, infestation occasionally reaching 50 % or more. This parasitoid is known to attack high density larval populations of *Pieris rapae* more heavily than low density ones (HARCOURT, 1966). By spreading her offspring around, an *A. cardamines* female may minimize the number killed by the Tachinid.
4. As the season progresses, some hostplant species senesce and become unavailable for oviposition. This results in a changing pattern of hostplants chosen by females (Figure 3) which may no longer oviposit on the early flowering *A. petiolata* or *Cardamine pratensis* but must select the persistent blooms of *Hesperis matronalis* and *Barbarea vulgaris* or the late-flowering *Rorippa sylvestris*. Where these foodplants are distributed in different micro-habitats, use of a sequence of hostplants will entail movement between these areas. For instance at Wolsingham *C. pratensis* occurs in very wet wooded areas, *B. vulgaris* and *A. petiolata* on the stones around the river, and *R. sylvestris* only on islands within the river itself. Females must move between all these areas in their search for foodplants during the season.

All these factors probably contribute to the higher mobility of female *A. cardamines*, and expansion along lines of favourable habitat (i.e. riverbanks) probably takes place by means of these local movements. One founder event was seen when, in 1978, a single female had flown along a small stream which connected with the river Tees at Middleton, Co. Durham. At the head of the stream, 2 km from the river, she had found a small patch of *C. pratensis* and had deposited there 37 eggs (only two survived to pupation and no adults were seen the following year). In this species, at least, there seems to be no basis to distinguish between migration (as defined as movement to a new population) and local, within-habitat movements. Longer distance movements in female *A. cardamines* seem to be nothing more than the upper end of a distribution of movements, which are all responses to the local environment.

Note that, although there are positive correlations in both sexes between pupal weight and adult wing span (Figure 4), there was no relationship between wing span and any of the parameters of movement studied: bigger animals did not fly faster or further (nor did they survive longer). This is in contrast to the suggestions of BAKER (1969) for *Pieris rapae* and *P. brassicae*; in these

truly migratory species adult size seems to contribute much more to patterns of motility than in the colonial *A. cardamines*. All these species are oligophagous upon Cruciferae, and produce pupae of differing weights when fed different hostplants (COURTNEY, 1981). The interesting possibility arises that animals feeding as larvae on different plants will have different capacities for movement. However these differences will only be important in migratory species: small individuals (particularly males) of more sedentary species may suffer little disadvantage.

Pieris napi (LINNÉ, 1758)

Pieris napi napi was studied in northern England in the years 1977–80, with some observations on *P. segonzaci* in the High Atlas, Morocco, in 1981. Studies on English populations rapidly showed that great differences in motility occurred between localities. Preliminary mark-recapture studies indicated, for instance, an overall recapture rate of 2 % in the population at Durham, as compared to a rate of 20.1 % at High Langdon, where a very large population flew over moorland in the years 1977 and 1978. LEES (1970) has suggested that two distinct forms of *P. napi* occur in Britain, respectively the normal *P. napi* of most of Europe, which occurs in the south and at low altitudes, and the post-glacial relict, identified by some as *P. n. thomsoni*, which occurs in Scotland and at high levels in the Pennines. LEES indicated that the upland populations he studied were colonial, with little migration, and felt that they had remained in these areas whilst the more southerly *P. n. napi* invaded lower levels following the amelioration of the post-glacial climate. Elsewhere I have argued that, although this view of several invasions of Britain by *P. napi* is tenable, the view of two distinct subspecies is untenable: every gradation occurs in the Durham area of the Pennines between single-brooded upland populations (with yellow females, "adalwinda" type androconial scales, and heavy pigmentation) and double-brooded lowland populations (white females, predominately "napi" type scales and light pigmentation). Voltinism itself appears to follow a mosaic pattern, rather than a strict association with altitude (E. LEES, pers. comm.). Nevertheless there did at first glance appear to be an association between altitude and movement pattern. Populations at high-level sites (e.g. High Langdon, 400 m) did indeed seem to be composed of individuals making short foraging flights in search of females, nectar sources, oviposition sites etc., whilst animals at lower levels (e.g. Durham, 37 m.) tended to fly strongly through the study area, stopping to nectar only periodically. Because of low returns with mark-recapture studies, movements of *P. napi* were investigated by means of the index of directionality devised by BAKER (1969) who noted that butterflies in voluntary displacement tend to follow direct paths of flight. The index then gives indication of the degree to which any particular orientation is preferred over all others. Directionality of *P. napi* flights was studied intensively in 1978, over a range of upland and lowland sites. Instead of choosing compass points, as did BAKER, the orientation of any major environmental feature present

(river, wall, forest edge etc.) was taken as one axis (the other axes being expressed relative to this). If no such axis was available, compass points were used. The results then give us an indication of the tendencies of butterflies to move in straight paths through an area: the more directional such paths, the larger the distances flown, and thus the greater is migration. The results for 1978 are plotted in Figure 5 against foodplant density at the study sites. Note that in two populations males seemed to show higher directionality than females (Table 3), because the females observed were in the characteristic "search mode" of flight, low above vegetation, looking for hostplants.

On closer examination, the observed association between movement behaviour and altitude proves to be at least partly the outcome of differing foodplant densities. Lowland populations occasionally show low directionality, when host-plant density is high (e.g. at Wolsingham), whilst individuals of high altitudes do show strong directionality when away from areas of abundant hosts. Thus this study provides little evidence of two forms of *P. napi* in Britain, differing in movement behaviour: animals in all areas appear to show displacement when hostplant abundance is low. This pattern seems to hold true for other populations of the *napi*-group (i.l.): *P. segonzaci* is usually localised to small discrete areas where *Nasturtium officinale* abounds. Away from these areas the butterfly flies more strongly. The observed low vagility of other upland *Pieris*, e.g. *P. bryoniae*, some Nearctic *P. napi* (F.S. CHEW, pers. comm.), may also be the result of high local foodplant abundance but generally low foodplant predictability outside these areas.

Discussion

It has been shown that females of *A. cardamines* range over wider areas than the males. Similar observations were made for *Euchloe ausonia* and *Euchloe belemia* at various sites in Morocco (1981–82), and for lowland populations of *P. n. napi* in Cheshire, England (1982). In all these species males seem to be localised in areas of high nectar abundance: in *A. cardamines* and *P. napi* these are also the areas of highest foodplant density. SHREEVE (1981) also records a higher recapture rate for males of lowland *P. napi*, *P. rapae* and *P. brassicae*, suggesting a higher rate of emigration by females of these species. In some other populations (*Zegris eupheme*, *Colotis evagore*, *P. segonzaci*) no such distribution of the sexes was noted. If, as suggested by BAKER (1969) and WIKLUND & AHRBERG (1978), movement patterns can be best understood in reference to the availability of resources (oviposition sites or females), what is the explanation of such differences between sexes and species?

The species under discussion are presented in Table 4, together with some indication of population structure and movement patterns. The species range from *Z. eupheme* which at Ifrane and Oukaimeden, Morocco, maintains discrete colonies associated with its hostplant *Isatis tinctoria*, to *Pontia daplidice*, which is found in almost every habitat in Morocco, existing always as a low

density vagrant. Several things may be immediately seen from Tab. 4; for instance it is clear that species with little or no differentiation between the habitats of the sexes are those with the most discrete populations (*Z. eupheme*, upland *P. napi* etc.) which are localised around discrete or isolated foodplant resources. Those species with strongest differentiation of the sexes (*E. belemia*, *E. ausonia*, *A. cardamines*) are those with intermediate levels of foodplant distribution and movement patterns. It is also readily seen that there is an association between population structure and the strategy of foodplant exploitation used by a species: colonial and sedentary species tend to be monophagous (*Z. eupheme*, *C. evagore*) or have restricted larval diets (*A. belia*, *P. bryoniae*, *P. segonzaci*). Polyphagous species (*E. ausonia*, *A. cardamines*, *P. n. napi*, *E. belemia*, *P. rapae*, *P. brassicae* und *Pontia daplidice*) tend to be much more wide-ranging. There is also a tendency for less vagile species to be associated with perennials, migratory species with annual hostplants. All these patterns are in agreement with the basic premise formulated by BAKER (1969) in regarding the resource as a primary determinant of the movement strategies of individuals and hence of population structure. Female butterflies searching for very clumped, isolated patches of a particular host species (e.g. *I. tinctoria*) should tend not to move outside the vicinity of the hosts. Here they will form a predictable resource for the males, which should occupy the same areas. On the other hand, females searching for more generally distributed hostplants of several species should show less localisation. However there will still be areas where more than average contacts with females may be obtained (field edges; areas with high hostplant density etc.) and males may be expected to congregate there. The situation with migratory species is less clear, although males should again tend to move less than females if they can anticipate the arrival of females in very favourable areas, as in the migratory *Inachis io* studied by BAKER (1972).

The observed patterns of movement of the Pierid butterflies shown in Table 4 do seem to agree with those predicted by BAKER's theories of the evolution of voluntary displacement in butterflies. Moreover, observed intra-specific variation in movement by *P. napi* in northern England also follows the pattern suggested – butterflies move through unfavourable habitats quickly. The means by which a butterfly recognises the quality of a habitat is largely unknown; plausible suggestions include the number of contacts with foodplants or conspecifics per unit time, and some directly perceived variables, correlated with "quality", such as shading. BAKER's theories fail however to take explicit consideration of the evolutionary advantages of voluntary displacement or sedentary lifestyles for males. Available evidence suggests that in some species, such as *A. cardamines*, the distribution of resources (females) favours a more aggregated distribution of males, and restricted movements by that sex. It is to be hoped that future studies will focus on sexual differences in flight activity and range, and on the cues used by either sex in assessing the suitability of a particular habitat.

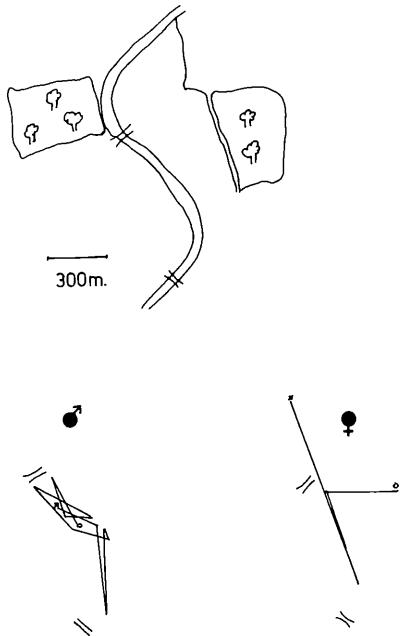


Figure 1



Figure 2

Figure 1:

Sketch map of the Durham study site, with examples of plotted recoveries of one marked individual from either sex of *A. cardamines*. The position of two bridges across the River Wear are marked in all three diagrams. Both individuals were marked during June 1979, and were recaptured over 11 (male) and 8 days (female). Positions of first (x) and last (o) capture are marked. Note that the male was captured only in a small area of riverside habitat, and that the female had crossed the open fields to move from the river to a small stream.

Figure 2:

The observed frequencies of plotted ranges R (from SCOTT, 1975) of *A. cardamines* at Durham.

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Durham
1978



Durham
1979

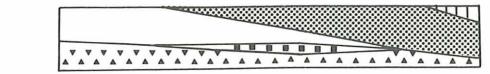
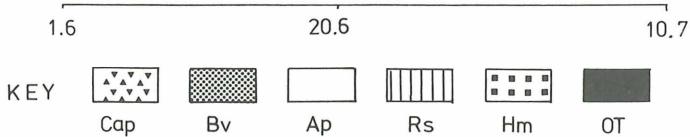


Figure 3

Figure 3:

Observed changes during the season in the use of hostplant species by *A. cardamines*. The percentage of eggs found on hostplants of various species are shown for three study sites per year. The category "others" is composed mostly of *Brassica rapa*, but with some *Sinapis arvensis*, *Capsella bursa-pastoris*, *Sisymbrium officinale*. Key: Ap. *Alliaria petiolata*, Bv *Barbarea vulgaris*, Cap *Cardamine amara* & *C. pratensis*, Hm *Hesperis matronalis*, Rs *Rorippa sylvestris*, Ot Others.

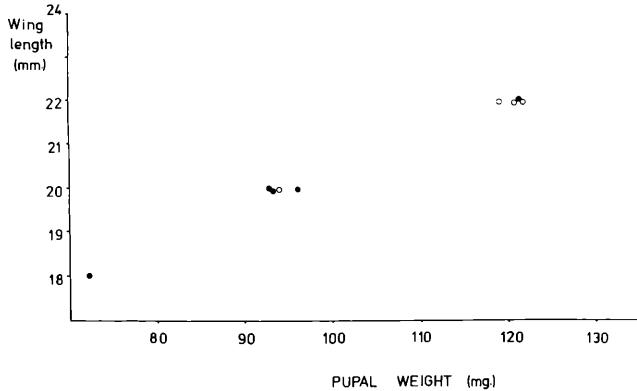


Figure 4

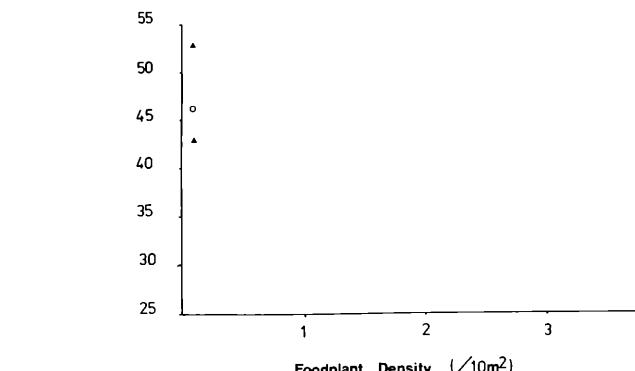


Figure 5

Figure 4:

Correlations between pupal weight and adult wing length (base to apex of forewing) in *A. cardamines*:

Males (open symbols) $r = 0.713$ $p < 0.001$

Females (closed symbols) $r = 0.919$ $p < 0.001$

Figure 5:

The proportion of *A. napi* individuals following the most preferred flight path in populations in northern England, related to host plant density. As per BAKER (1969), proportions may range from .25 (no preference amongst the four axes) to 1.0 (uniform directionality of movement). Most observations from 1978

Closed circles: lowland populations (< 150 m.) 1st brood.

Open circles: lowland, 2nd brood.

Triangles: upland, single brooded.

	Males	Females	
	1977	1978	1979
No. of animals	All years summed		
marked	127	168	145
mean R	211.5	184.2	483.5
mean D	247.0	253.5	751.4
mean V	97.8	88.7	150.1
			104.5

Table 1:

Values of parameters for the flight behaviour of *A. cardamines* at Durham 1977–79, following the procedure of SCOTT (1975). R = Distance between two furthest points of capture (m.). D = Sum of all distances between points of capture (minimum flight distance). V = D/lifespan (days) from first to last capture (minimum speed of movement).

No. of females observed	22
Total period of observations	105 mins.
X Period of observation	4.8 mins.
No. of occasions on which females left riverbanks	15

Table 2:

Observed behaviour of *A. cardamines* at Durham in 1979. During equivalent observation on males, no individual was seen to leave the riverbanks area

Table 3:

Proportion of *A. napi* flying in the preferred flight path.

	Wolsingham				Langwathby
	1977		1978		1978
	<u>1</u>	<u>2</u>	<u>1</u>	<u>2</u>	<u>2</u>
Males	.33	.32	.31	.38	.35
Females	.30	.29	.30	.33	.29

Colonial	Sedentary	Vagile	Migratory
<i>Zegris eupheme</i>	<i>Anthocharis belia</i>	<i>Euchloe belemia</i>	<i>Pieris rapae</i>
	<i>Colotis evagore</i>	<i>E. falloui</i>	<i>P. brassicae</i>
		<i>Elphinstonia charlonia</i>	<i>Pontia daplidice</i>
	<i>Pieris bryoniae</i>	<i>P. n. napi</i>	
	<i>P. segonzaci</i>		
	" <i>P.n. thomsoni</i> "		
	<i>E.a. ausonia</i>	<i>E.a. simplonia</i>	
	<i>A. cardamines</i> (northern)	<i>A. cardamines</i> (northern)	

Table 4:

Population structure and movement patterns in Pierids feeding on Cruciferae, Resedaceae or Capparidaceae. "Sedentary" populations are localised around particularly favourable areas, but with some movement away from these. "Vagile" populations are more generally mobile. Note that southern English populations of *A. cardamines* are more mobile than northern butterflies.

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